Global Ecology and Conservation 17 (2019) e00541

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Short Communication

Bears without borders: Long-distance movement in human-dominated landscapes

Kamil A. Bartoń [a, *, 1], Tomasz Zwijacz-Kozica [b], Filip Zięba [b], Agnieszka Sergiel [a], Nuria Selva [a, 1]

[a] Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, 31-120, Kraków, Poland
[b] Tatra National Park, Kuźnice 1, 34-500, Zakopane, Poland

A R T I C L E I N F O

Article history:
Received 26 November 2018
Received in revised form 22 January 2019
Accepted 22 January 2019

Keywords:
Long-distance dispersal
Movement
Ursus arctos
Large carnivores
Transboundary cooperation
Conservation policies

A B S T R A C T

Conservation of wide-ranging species and their mobility is a major challenge in an increasingly fragmented world. Species are traditionally viewed as static conservation targets and the importance of securing long-distance movement of individuals is still underappreciated in conservation and policy. Here, we investigated large carnivore movements in humanized landscapes of Europe. We describe the movement of 6 GPS-tracked male brown bears, including one of the longest dispersal events recorded in this species. We looked at the relationships of bear movement paths with country borders, roads, built-up areas and habitat composition. The daily distance of resident individuals was 5.5 ± 4.4 km and almost twice as long in the dispersing subadult (9.3 ± 6.4 km). Maximum displacement of the disperser was 360 km (compared to 43.3 ± 13.0 km in resident bears). The resident bears moved within less than 10 km to built-up areas, while the dispersing bear stayed mostly at larger distances. The bears also frequently crossed roads (0–31 per month) and state borders (0–14 per month). The dispersing bear moved through four countries. A review of 29 cases and studies of large carnivore long-distance movements in Europe showed that transboundary movement represented over 96% of all cases; 9 extended over different populations and 10 over recolonization areas. Most documented cases of long-distance dispersal (52% of 21 individual cases) ended with the death of the animal (82% of confirmed deaths were human-caused, 46% were legal killings) before it could reproduce. Reproduction was documented only in 2 of the individual cases. We emphasize high conservation value of long-distance dispersers in large carnivore populations and the need to reevaluate how they are viewed and managed. We urge to consider wide-ranging, transboundary movements in conservation policies.

1. Introduction

Movement of animals between and within populations is crucial for the persistence of populations and functioning of ecosystems (Clobert et al., 2012). Human activity and infrastructure affect animal movement by creating barriers, altering

* Corresponding author.
E-mail addresses: kbarton@iop.krakow.pl (K.A. Bartoń), tzwijacz@tpn.pl (T. Zwijacz-Kozica), fzieba@tpn.pl (F. Zięba), sergiel@iop.krakow.pl (A. Sergiel), nuria@iop.krakow.pl (N. Selva).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.gecco.2019.e00541

and fragmenting habitats (e.g. Seidler et al., 2015; Tucker et al., 2018). Reduction in movements of mammals worldwide has been attributed to behavioural changes and exclusion of wide-ranging species from areas with higher human impact (Tucker et al., 2018). In humanized landscapes, long-range movement is particularly important to maintain gene flow between isolated populations (Elliot et al., 2014; Rabinowitz and Zeller, 2010). As the world becomes increasingly fragmented, both physically and politically (e.g. Linnell et al., 2016), there is an urgent need to improve our knowledge on wide-range movement behaviour of animals to inform conservation policies (Caro and Sherman, 2012; Lambertucci et al., 2014).

Large carnivores are especially vulnerable to the effects of anthropogenic landscapes on their movements (Ripple et al., 2014), due to their low densities and large spatial requirements, including long-distance dispersal (Gittleman et al., 2001; Santini et al., 2013). Dispersal is the movement from the site of birth to the site of potential reproduction (natal dispersal) or between sites of reproduction (breeding dispersal; Clobert et al., 2012). For the purpose of this study, we defined "long-distance" as a landscape- rather than as a species-specific quality, to describe a relocation much beyond the natal patch and usually involving crossing anthropogenic borders or barriers. In Europe, where large carnivore populations are recovering and expanding into new areas (Chapron et al., 2014), long-distance dispersal events are particularly challenging, due to high habitat fragmentation and human density. These events are considered rare and difficult to record in elusive and wide-ranging species (Trakhtenbrot et al., 2005), therefore, long-distance dispersal success (i.e. reproduction confirmed) in large carnivores has been rarely evaluated (Kojola et al., 2006; Zimmermann et al., 2005).

In this study, we focus on the movement behaviour of brown bears *Ursus arctos*, the most abundant large carnivore in Europe (Chapron et al., 2014). They are also the most omnivorous, relying on both animal and vegetal food resources (ungulates represent 10.5% [0–33%] of their diet; Bojarska and Selva, 2012; Niedziałkowska et al., 2019). Like in most large carnivores, brown bear dispersal is male-biased: males disperse farthest as subadults, while females are highly philopatric (Støen et al., 2006). We describe the movement of six brown bear males in central Europe, including a long-distance dispersal event. This allows us to compare patterns of movement during dispersal and non-dispersive movement. Dispersing bears may face more difficulties than resident ones as they more often move in a novel, potentially more humanized habitat, encountering physical and political barriers, as well as different protection regimes.

By assessing the differences in movement patterns of dispersing and resident bears at a landscape scale, regarding interactions of individuals with landscape features (road and border crossings, and habitat composition), we seek to gain insights into the movement ecology of this wide-ranging species in strongly human-altered landscapes. To get a broader view of the ecological process, we compiled information on long-distance dispersal events of large carnivores documented in Europe, including the populations connected, displacement distance and fate of the animal. Finally, we discuss the importance of considering long-distance dispersers, wide-ranging movements, and behavioural diversity in general, in conservation policies, and emphasize the need for transboundary cooperation and coordinated conservation efforts.

2. Methods

2.1. Study area and population

The Carpathian brown bear population is the second largest in Europe and extends over six countries. It is divided into three population segments; the connectivity between the western and eastern segments is quite limited (Selva et al., 2011; Straka et al., 2012). Infrastructure development is considered the main threat for the persistence of this population; the lack of transboundary cooperation in management has also been pointed as an issue (Selva et al., 2011). The brown bear population in the Tatra Mountains represents the core area of the western segment of the Carpathian population and it is split between Poland and Slovakia. Most of the area is protected by two national parks.

2.2. Movement data

In 2014–2016 we tracked six male bears fitted with GPS transmitters (5 adults and 1 subadult) captured in the Tatra Mountains. The bears were captured in box or Aldrich traps, immobilized and fitted with GPS-GSM/Iridium collars equipped with a drop-off system (Lotek Wildcell M/MG/GPS4400, Vectronic Vertex Plus). We followed the biomedical protocols by Arnemo et al. (2011). Tracking duration of an individual ranged from 252 to 633 days (mean 399.2 days). Majority of location fixes (83%) were taken at 30 min intervals (range: 30–240 min).

To characterize movement patterns, for each recorded individual's path we calculated total distance covered, daily distances, and daily and maximum displacement. The daily figures are based on "bear days" (24-h periods starting from 12:00), as the animals' activity drop was deepest around midday; a pattern also found in other populations (Ordiz et al., 2014). The maximum displacement was calculated as a Euclidean distance between the two locations farthest apart. Daily displacement was a straight line distance between two locations at the beginning and end of each "bear day". To obtain a measure of path straightness, we calculated a ratio of daily displacement to daily distance. As the locations spanned a large longitudinal extent, we adjusted Central European Time locally by 4 min per degree longitude. We limited the calculations to "active periods", i.e. we excluded winter denning (identified as continuous periods when there was either no movement or occasional, short displacements < 1 km per day).

2.3. Landscape data

To estimate habitat composition around the movement paths, we extracted percentages of land cover types within 500 m around each recorded bear position. We calculated the overall proportion of land cover as the mean of the proportions for each position, weighted by the time interval between the locations in order to account for uneven time periods between position fixes. We also calculated the distance to the nearest built-up/urban area along the paths (as a distance to the map pixel centres). We used the ESA CCI Land Cover map (version 2), at 300 m spatial resolution (Li et al., 2018; downloaded from https://www.esa-landcover-cci.org/). The maps' original UN Land Cover Classification System (Gregorio, 2005) was simplified to 7 categories (see Table A1 for details). We also calculated the frequency of country border and road crossings in each bear's movement path. The latter was done using datasets from OpenStreetMap (OpenStreetMap contributors, 2015), including road categories from "motorways" to "tertiary roads".

2.4. Review of long-distance movement of large carnivores in Europe

Information on long-distance movement (using an arbitrary threshold of 50 km, for discussion see Jordano (2017) or Nathan et al. (2003)) records for large carnivores in Europe (brown bear, wolf *Canis lupus*, and lynx *Lynx lynx;* wolverine *Gulo gulo* was not included, because of the species limited distribution in Europe) was extracted from scientific papers, technical reports and websites (see Table B.1 for details on the data collected). We compiled a total of 29 records including individual cases of long-distance movement (N = 21) and population studies (N = 8).

3. Results

3.1. Long-distance dispersal

We recorded bear movement paths ranging from 904 to 3640 km (mean 1849.2 km, Table 1). Among the six tracked individuals, only the subadult BI4 (nicknamed "Iwo") pursued a long-range movement with a maximum displacement of 360 km, which is approximately eight times the distance for non-dispersing bears (mean 43.3 ± 13.0 km, N = 5, see Fig. A.1). During the first year of tracking, Iwo carried out several loops around the central area, then, in the second year, engaged in dispersal (Fig. 1, lower panel). The dispersal commenced end of April 2015 and lasted at least 10 months, after which the collar dropped as programmed and was recovered. The movement path consisted of conspicuously directional sections (>100 km long) and occasional layovers with a movement pattern similar to that of the resident bears. A 110 km extent in the west of Ukraine was traversed by the bear three times along similar routes (with the subsequent paths max. 15 km apart, see lower panel of Fig. 1).

3.2. Movement patterns of dispersing vs resident males

The active period lasted from March to November, but could extend to as late as to early January (see Fig. A.1). The daily distance in resident individuals ranged from 4.0 to 8.7 km (grand mean of bear-years 5.5 ± 4.4 km, see Table 1). The subadult Iwo moved similar distances in the first year of tracking (daily mean 5.3 ± 3.3 km), but nearly twice as much during the dispersal in the second year (9.3 ± 6.4 km). The maximum daily distance travelled was largest in Iwo (particularly during

Table 1
Basic statistics for the recorded brown bear movement tracks: daily distances and daily displacement, mean number of country border and road crossings per month, and maximum displacement for the path. The figures are given per year and for the whole tracking period (in bold). See "Methods" for details on how the statistics were calculated.

Bear ID	Year/tracking period	N days tracked	Daily distance (km)		Daily displacement (km)		Overall maximum displacement (km)	Monthly average number of crossings	
			Mean ± SD	Max.	Mean ± SD	Max.		Country borders	Roads
BA1	2013	176	5.0 (±3.2)	12.8	2.6 (±2.2)	11.0	22	0	18.8
BF3	2014	214	4.0 (±3.3)	17.1	3.0 (±2.9)	16.1	57	2.3	8.8
BE6	2014	147	3.6 (±2.4)	11.4	2.0 (±2.0)	9.7	44	1.0	3.9
	2015	38	3.9 (±3.3)	13.0	2.2 (±2.8)	11.4	30	3.2	13.6
	2014–2015	**185**	**3.7 (±2.6)**	**13.0**	**2.0 (±2.2)**	**11.4**	**48**	**1.5**	**5.9**
BI4 ("Iwo")	2014	169	5.3 (±3.3)	20.4	2.6 (±3.1)	18.1	78	0.7	31.0
	2015	286	9.3 (±6.4)	34.8	5.1 (±5.6)	29.7	312	4.8	21.3
	2014–2015	**455**	**7.8 (±5.8)**	**34.8**	**4.2 (±5.0)**	**29.7**	**360**	**3.3**	**24.9**
BH2	2014	42	4.3 (±2.8)	11.5	2.6 (±2.2)	7.5	19	0	0
	2015	164	6.3 (±3.7)	17.6	2.8 (±2.8)	14.5	46	1.5	11.5
	2016	73	4.5 (±4.0)	16.0	2.3 (±2.3)	9.0	19	2.5	0
	2014–2016	**279**	**5.5 (±3.8)**	**17.6**	**2.6 (±2.6)**	**14.5**	**47**	**1.5**	**6.8**
BW5	2015	199	8.4 (±4.9)	25.4	2.9 (±3.0)	14.0	41	6.7	13.3
	2016	170	9.3 (±5.7)	28.5	3.3 (±2.7)	11.2	29	14.1	21.8
	2015–2016	**369**	**8.8 (±5.3)**	**28.5**	**3.1 (±2.8)**	**14.0**	**42**	**10.1**	**17.2**

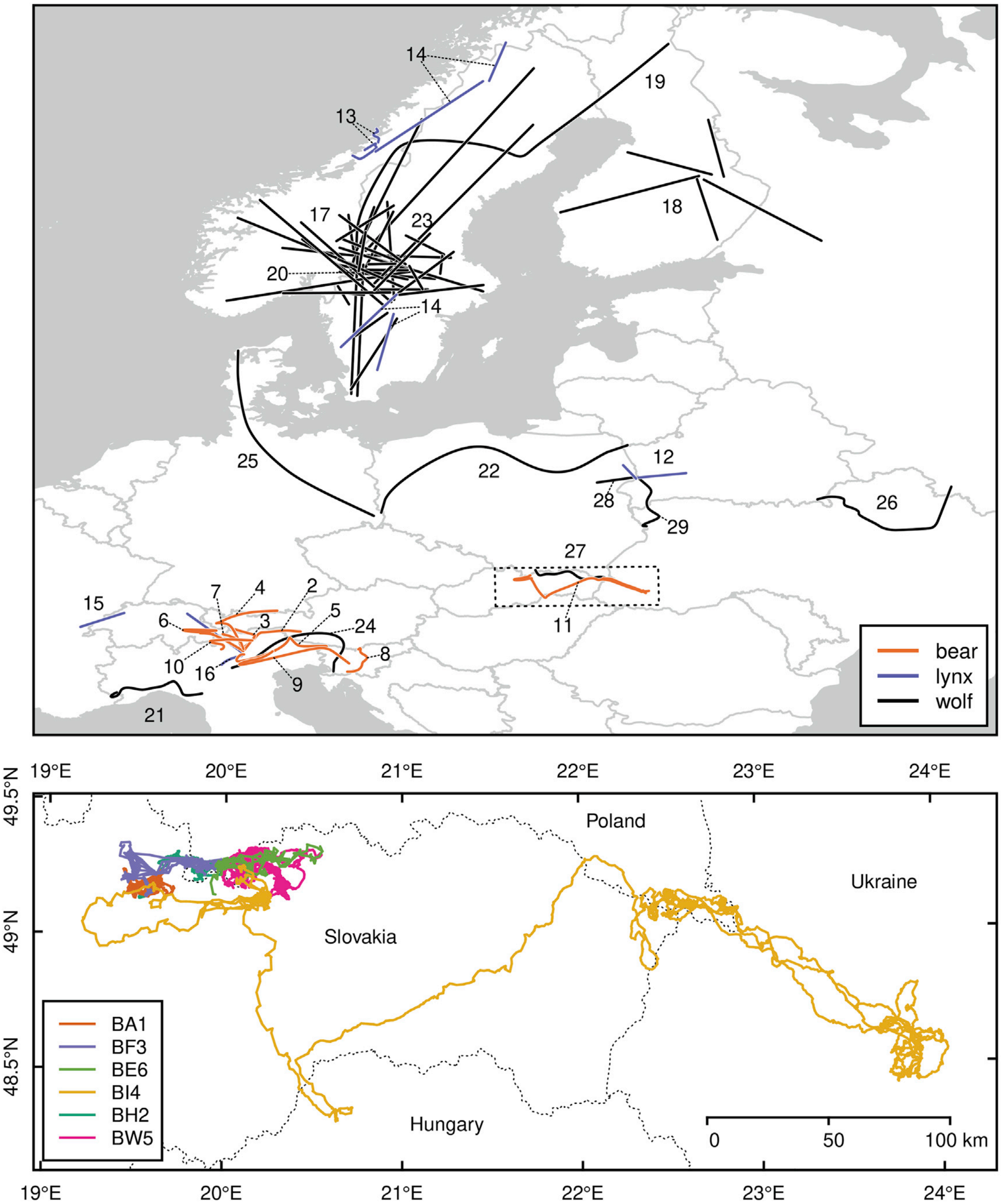

Fig. 1. *Upper panel*: Large carnivore long-distance dispersal events documented in Europe (Table B.1). Where such information was available, a (simplified) route is drawn, otherwise the straight lines connect starting and end locations. Numbers refer to the first column in Table B.1. The dotted line rectangle outlines the study area shown in the lower panel. *Lower panel*: Recorded movement paths of the six GPS-collared male bears in the northern Carpathian region. Grey (upper panel) and dotted lines (lower panel) denote country borders.

dispersal) and BW5, respectively 34.8 and 28.5 km. In the other resident bears it ranged from 13 to 18 km (Table 1). The maximum displacement in the recorded paths of the adult bears ranged from 19 to 57 km (mean 34.1 ± 13.0 km), while in the dispersing individual's path it was 360.2 km (Table 1).

Examination of path straightness (Fig. A.2) showed that some resident bears moved in a fairly straight manner much of the time (BF3, BE6), while others tended to move more tortuously and return close to previous sites. This pattern was most apparent in BW5, a resident bear who moved the longest daily distances (similar to those of the dispersing Iwo), but whose mean daily displacement was close to those of the other resident bears (see Table 1). Unlike the adult resident bears, subadult

Iwo had a clearly bimodal pattern in path straightness, which supports the observation of the two types of movement behaviour (e.g. Patterson et al., 2008; see Fig. A.2).

3.3. Landscape structure

The habitat around the majority of recorded bear locations consisted mostly of tree cover (76–97%), considerably less of grasslands (1–16%) and crops (1–6%, Fig. A.3). A notable difference was in Iwo's locations in the first tracking year, where grasslands and croplands formed 57% of the surrounding habitat, while during dispersal in the second year these habitat types constituted only 10% of the surrounding habitat.

All fixes of resident bears were located closer than 10 km from built-up areas (the minimum distance during "bear day" was <2 km on 24–71% of tracking days), including hibernation places. Before his dispersal phase, Iwo kept relatively close to built-up areas (<2 km on 84% of days), also hibernating in the proximity of buildings (at 3–4 km). Then, during most of the dispersal phase, he kept at much larger distances (>10 km on 37% of days) to built-up areas, less often staying at below 2 km (23% of days).

3.4. Border and road crossings

The resident bears frequently crossed state borders, moving between Poland and Slovakia (except BA1). On average, resident individuals crossed a border every two weeks (Table 1). Iwo crossed country boundaries on average once per five weeks in the first year, and once per week in the second year (during the dispersal). During the tracking period this bear moved through four countries (see lower panel of Fig. 1). On average, Iwo crossed roads more often before his dispersal phase (31 crossings/month) than during dispersal (21 crossings/month), and overall more often than resident bears (max. 18.8 crossings/month in BA1). He was the only tracked individual to cross motorways, which he did three times during the dispersal, likely using wildlife passages or passing under bridges (see Fig. A.4).

3.5. Review of long-distance movement of large carnivores in Europe

All but one of the collected studies and cases for large carnivores in Europe included transboundary movement (Table B.1). Of these, nine movement paths extended over two (sub)populations, and ten over areas without a permanent occurrence of the species. In general, wolves were the species moving the greatest distances: displacements >500 km were recorded for two individuals.

Effective dispersal (i.e. dispersal followed by successful reproduction) was confirmed only in 2 (possibly 3) of the 21 individual cases (10–14%, Table B.1), all in wolves. The death of the animal during the tracking period was documented in 52% of the individual cases (n = 11); in 38% (n = 8) the fate of the animal was unknown, and in 10% (n = 2) the animal was still alive at the end of the study period. Among the confirmed deaths of long-distance dispersers, 82% (n = 9) were human-caused (46% killed legally, 18% illegally, and in 18% legality of the killing was unspecified), and 18% of the confirmed deaths (n = 2) were due to natural or unknown reasons. Traffic collisions (car and train) during long-distance dispersal were documented in two brown bears, both animals survived the accident.

The population studies did not restrict to long-distance dispersers (see Table B.1), and only two provided information on reproduction success and fate of the tracked individuals. In Finland, reproduction was confirmed in 33% of the wolves that dispersed (10 out of 30, both short- and long-distance dispersers) and in 45% of those with known fates for at least two years after departure (10 out of 22; Kojola et al., 2006). Among the wolves with known fates, 27% (6 out of 22) were shot before reproducing (Kojola et al., 2006). In the case of the lynx in the Swiss Alps, among 27 juveniles whose dispersal characteristics were documented, 22% (n = 6) reproduced confirmedly, and 22% died (n = 6) during the study period. Of these 27 dispersers, only 26% (n = 7) moved more than 50 km, of which one reproduced confirmedly and one was killed illegally (Zimmermann et al., 2005). None of the bear population studies we collected gave information on the reproduction or fate of the dispersers.

4. Discussion

Over 12% of the world's vertebrates are known to make long-distance movements (Runge et al., 2014). Highly mobile species occur everywhere and, even in highly human-dominated areas, such as Europe, large carnivores still perform long-distance movements and, occasionally, can reproduce successfully. Evidence of such movements is mostly available from intensively monitored populations, for instance, bears in Trentino, Italy. These events may be, therefore, more common than conventionally thought. Recent advances in animal tracking technologies, genetic tools, phototrapping and stable isotope analysis allow for increasing records of long-distance movements and improving our understanding of related processes (e.g. Kays et al., 2015), such as the ongoing expansion of large carnivores in Europe (Chapron et al., 2014). Knowledge of long-distance movements, particularly if nomadic or more erratic, and the identification of connectivity problems are crucial to design effective conservation strategies for mobile species. It is, therefore, essential to publish detailed information on every long-distance dispersal event, and we strongly encourage researchers and managers to share these data. Experience from single events (e.g. Rosen and Bath, 2009; see also references in Table B.1) helps to understand why dispersal journeys end successfully or not.

Our bear movement data emphasises the potentially important role of subadult males in connecting bear subpopulations. Iwo's dispersal shows that the western and eastern population segments in the Carpathians, genetically differentiated after a century of isolation (Straka et al., 2012), may maintain connectivity, although not necessarily through the corridor derived from movement models (Ziółkowska et al., 2016), which is the shortest route and was proposed as a target for conservation actions (Selva et al., 2011). The presented case of bear dispersal confirms the importance of road wildlife passages in supporting species movements (Fig. A.4). The dispersing bear's apparent avoidance of built-up areas underlines the need to carefully plan housing development, also in areas where large carnivores are not present permanently, in order to support connectivity of large carnivore populations and habitat quality (Fernández et al., 2012; Ziółkowska et al., 2016). Due to the disperser's tendency to stay close to human settlements during his resident phase, his removal had been considered by managers in Slovakia. However, using human settlements as refuges is a natural and adaptive behaviour in brown bears, and does not necessarily indicate a problem animal (Elfström et al., 2014). Thus, a proper strategy for management of possible damages caused by long-distance dispersers is necessary. Moreover, management policies can jeopardize long-range movements since vagrants and dispersing subadults are often the target of hunting or culling practices established in large carnivore management plans (e.g. 70% of the bears shot in Slovenia were subadults ≤5-year-old, Jerina et al., 2003). Over half of the long-distance dispersers die on the way, before having the opportunity to reproduce, which may have negative consequences for restoring and maintaining population connectivity. To improve population connectivity, reducing lethal management pressure seems a more feasible policy in Europe than to reduce the human footprint (Quevedo et al., 2019).

Out of 33 populations of large carnivores in Europe, 28 are transboundary (Blanco, 2012; Chapron et al., 2014). Twenty-eight of the 29 records of long-distance dispersal listed in Table B.1 involved border crossing. Similarly, all except one of the bears studied by us in the northern Carpathians regularly crossed country borders. In the case of Iwo, the frequency of border crossings during dispersal increased almost 7-fold, compared to the pre-dispersal phase. As large carnivores move across political borders, they are exposed to different rules and legislation, and the lack of coordinated actions on either side of a border can undermine local conservation efforts and the efficiency of management. The bears studied by us moved between countries with different management and conservation status for the species (Selva et al., 2011): strictly protected (Poland, Ukraine) but with different level of law enforcement; protected, but with culling (Slovakia); and without a brown bear population, and thus, no conservation status assessment or strategy (Hungary). Transboundary cooperation in Europe happens mostly informally at the technical level, i.e. the experts from different countries work together in an unofficial way, but usually there is no formal cooperation among conservation agencies or at the political level (Blanco, 2012). This unofficial network of experts across countries was crucial during the dispersal of Iwo (e.g. to manage and inform the public about the presence of the bear in Hungary or to recover the transmitter in Ukraine), and open communication flow was kept as the animal was moving from one country to other. The mission impossible was to re-trap the bear to replace the collar and continue gaining information about his dispersal. This and the other cases collected in Table B.1 illustrate the costs that socio-political boundaries impose on conservation by fragmenting ownership, governance, and management (Dallimer and Strange, 2015). In this sense, the recent proliferation of border fences as a response to the refugee crisis or other security purposes is highly detrimental for conservation (Linnell et al., 2016). They do not only kill wildlife which gets entangled in razor wires, but also pose an impassable barrier to animal movements and, hence, habitat connectivity.

The conservation of highly mobile species and the ecological processes related to their movement pose a major challenge. Current conservation planning typically views species as static targets and mostly fails to address the spatiotemporal dynamism of animal distributions (Bull et al., 2013; Davis and Watson, 2018; Runge et al., 2014). The importance of securing the success of long-distance dispersal and wide-ranging movements of large carnivores (and highly mobile species, in general) for population connectivity is still under-appreciated and remains one of the main knowledge gaps in conservation (Driscoll et al., 2014; Trakhtenbrot et al., 2005). Preserving daily and dispersive movements of highly mobile species over large distances and political borders also requires international collaboration and that the scale of management will match the scale of the conservation issue (Dallimer and Strange, 2015; Kark et al., 2015). Mobile protected areas that “move” with the target species itself, permanently or during vulnerable periods, have been proven valuable in the conservation of marine and migratory species (Bull et al., 2013). A similar approach could also be effective in the case of long-distance-dispersing or vagrant individuals of large carnivores, which should be granted a special conservation status as mobile conservation targets. Such individuals have a disproportionately high conservation value but are often killed, both legally and illegally. Almost half of the deaths of long-distance dispersers in Europe were legal (Table B.1). Special protection of those individuals during hazardous dispersal journeys could support their survival and improve dispersal success, currently regarded as extremely low. It could also foster the implementation of non-lethal management measures (e.g. related to damage mitigation) and the modification of the classification of risk assessments and recommended actions in management plans when the individual in question is a long-distance disperser. Given the importance of long-distance dispersal for the functional connectivity of large carnivore populations in fragmented landscapes, such dynamic conservation strategies are definitively worthy to start to be considered (Reynolds et al., 2017). Vagrants and long-distance dispersers may also represent the forerunners of climate adaptation (Davis and Watson, 2018). Conservation managers and policymakers should reconsider how these animals are viewed and managed, and how they could be explicitly considered in the law.

Conserving animal movement as a process is a big challenge, particularly of wide-ranging species in fragmented landscapes. There are several steps to be taken in this direction concerning large carnivores: (1) gaining and sharing knowledge on why, when and how they move, particularly on long-distance dispersal events; (2) improving international cooperation (e.g. establishing periodical meetings of expert teams for large regions or populations); and using long-distance dispersal events as a unique opportunity for strengthening transboundary collaboration and raising public awareness of large carnivore conservation; (3) elimination of barriers (e.g. border fences); and mitigation of their effects (e.g. road wildlife passages); (4) proper habitat management, mostly through careful planning of urban development, also in areas where the species do not permanently occur but can act as connectivity corridors; (5) efficient management of damages during dispersal events and special treatment of long-distance dispersers in management plans; and (6) recognize the high importance of long-distance dispersers and vagrants and consider them as mobile conservation targets, both explicitly in the law and practically in the way they are perceived and managed.

Acknowledgements

This study was financed by the National Science Centre grant no. 2015/16/S/NZ8/00158 to KB and grant no. 2016/22/Z/NZ8/00121 (BearConnect) through the ERA-NET BiodivERsA call, and the National Centre for Research and Development grant POLNOR/198352/85/2013 (GLOBE). All captures and handling were approved by the Polish authorities (no. DOP-OZ.6401.08.2.2013.ls, DOP-OZ. 6401.08.2.2013.ls.1 and DZP-WG.6401.08.8.2014.JRO), Polish ethical committee (no. 21/2013 and 101/2014), and Slovak Ministry of Environment (MŽP SR č. 3555/2012-2.2). We thank the staff of Polish and Slovak Tatra National Parks for their help in bear trapping. KB and NS conceived and designed the study; KB analysed the data and prepared the figures; NS compiled the published dispersal data; NS, AS, FZ, TZK collected the data; KB and NS wrote the first version of the manuscript, which was then revised by all authors. All authors read and approved the final manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00541.

References

Arnemo, J.M., Evans, A., Fahlman, A.A., 2011. Biomedical Protocols for Free-Ranging Brown Bears. Wolves Wolver. In: Lynx Nor. Dir. Nat. Manag. Trondheim 2011.

Blanco, J.C., 2012. Towards a population level approach for the management of large carnivores in Europe: challenges and opportunities (Report for the European Commission).

Bojarska, K., Selva, N., 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mamm Rev. 42, 120–143. https://doi.org/10.1111/j.1365-2907.2011.00192.x.

Bull, J.W., Suttle, K.B., Singh, N.J., Milner-Gulland, E.J., 2013. Conservation when nothing stands still: moving targets and biodiversity offsets. Front. Ecol. Environ. 11, 203–210. https://doi.org/10.1890/120020.

Caro, T., Sherman, P.W., 2012. Vanishing behaviors. Conserv. Lett. 5, 159–166. https://doi.org/10.1111/j.1755-263X.2012.00224.x.

Chapron, G., Kaczensky, P., Linnell, J.D.C., Arx, M. von, Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553.

Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), 2012. Dispersal Ecology and Evolution. Oxford University Press.

Dallimer, M., Strange, N., 2015. Why socio-political borders and boundaries matter in conservation. Trends Ecol. Evol. 30, 132–139. https://doi.org/10.1016/j.tree.2014.12.004.

Davis, R.A., Watson, D.M., 2018. Vagrants as vanguards of range shifts in a dynamic world. Biol. Conserv. 224, 238–241. https://doi.org/10.1016/j.biocon.2018.06.006.

Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., Edworthy, A., Evans, M.J., Gibson, R., Heinsohn, R., Howland, B., Kay, G., Munro, N., Scheele, B.C., Stirnemann, I., Stojanovic, D., Sweaney, N., Villaseñor, N.R., Westgate, M.J., 2014. The Trajectory of Dispersal Research in Conservation Biology. Systematic Review. PLoS One 9, e95053. https://doi.org/10.1371/journal.pone.0095053.

Elfström, M., Zedrosser, A., Støen, O.-G., Swenson, J.E., 2014. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mamm Rev. 44, 5–18. https://doi.org/10.1111/j.1365-2907.2012.00223.x.

Elliot, N.B., Cushman, S.A., Macdonald, D.W., Loveridge, A.J., 2014. The devil is in the dispersers: predictions of landscape connectivity change with demography. J. Appl. Ecol. 51, 1169–1178. https://doi.org/10.1111/1365-2664.12282.

Fernández, N., Selva, N., Yuste, C., Okarma, H., Jakubiec, Z., 2012. Brown bears at the edge: Modeling habitat constrains at the periphery of the Carpathian population. Biol. Conserv. 153, 134–142. https://doi.org/10.1016/j.biocon.2012.04.013.

Gittleman, J.L., Funk, S.M., MacDonald, D.W., Wayne, R.K., 2001. Carnivore Conservation. Cambridge University Press.

Gregorio, A.D., 2005. Land Cover Classification System: Classification Concepts and User Manual : LCCS. In: Food & Agriculture Org.

Jerina, K., Debeljak, M., Džeroski, S., Kobler, A., Adamič, M., 2003. Modeling the brown bear population in Slovenia: A tool in the conservation management of a threatened species. In: Ecol. Model., ISEM The third European Ecological Modelling Conference, vol. 170, pp. 453–469. https://doi.org/10.1016/S0304-3800(03)00245-X.

Jordano, P., 2017. What is long-distance dispersal? And a taxonomy of dispersal events. J. Ecol. 105, 75–84. https://doi.org/10.1111/1365-2745.12690.

Kark, S., Tulloch, A., Gordon, A., Mazor, T., Bunnefeld, N., Levin, N., 2015. Cross-boundary collaboration: key to the conservation puzzle. In: Curr. Opin. Environ. Sustain., Sustainability governance and transformation, vol. 12, pp. 12–24. https://doi.org/10.1016/j.cosust.2014.08.005.

Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. Science 348, aaa2478. https://doi.org/10.1126/science.aaa2478.

Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., Ronkainen, S., 2006. Dispersal in an expanding wolf population in Finland. J. Mammal. 87, 281–286. https://doi.org/10.1644/05-MAMM-A-061R2.1.

Lambertucci, S.A., Alarcón, P.A.E., Hiraldo, F., Sanchez-Zapata, J.A., Blanco, G., Donázar, J.A., 2014. Apex scavenger movements call for transboundary conservation policies. Biol. Conserv. 170, 145–150. https://doi.org/10.1016/j.biocon.2013.12.041.

Li, W., MacBean, N., Ciais, P., Defourny, P., Lamarche, C., Bontemps, S., Houghton, R.A., Peng, S., 2018. Gross and net land cover changes in the main plant functional types derived from the annual ESA CCI land cover maps (1992–2015). Earth Syst. Sci. Data 10, 219–234. https://doi.org/10.5194/essd-10-219-2018.

Linnell, J.D., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinsek, T., Potocnik, H., 2016. Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia? PLoS Biol. 14, e1002483. https://doi.org/10.1371/journal.pbio.1002483.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E., Cain, M.L., 2003. Methods for estimating long-distance dispersal. Oikos 103, 261–273. https://doi.org/10.1034/j.1600-0706.2003.12146.x.

Niedziałkowska, M., Hayward, M.W., Borowik, T., Jędrzejewski, W., Jędrzejewska, B., 2019. A meta-analysis of ungulate predation and prey selection by the brown bear Ursus arctos in Eurasia. Mammal Res. 64, 1–9. https://doi.org/10.1007/s13364-018-0396-7.

OpenStreetMap contributors, 2015. Planet dump [Data file from 2015]. retrieved from. https://planet.osm.org.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J.E., Støen, O.-G., 2014. Brown bear circadian behavior reveals human environmental encroachment. Biol. Conserv. 173, 1–9. https://doi.org/10.1016/j.biocon.2014.03.006.

Patterson, T., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State–space models of individual animal movement. Trends Ecol. Evol. 23, 87–94. https://doi.org/10.1016/j.tree.2007.10.009.

Quevedo, M., Echegaray, J., Fernández-Gil, A., Leonard, J.A., Naves, J., Ordiz, A., Revilla, E., Vilà, C., 2019. Lethal management may hinder population recovery in Iberian wolves. Biodivers. Conserv. 28, 415–432. https://doi.org/10.1007/s10531-018-1668-x.

Rabinowitz, A., Zeller, K.A., 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biol. Conserv. 143, 939–945. https://doi.org/10.1016/j.biocon.2010.01.002.

Reynolds, M.D., Sullivan, B.L., Hallstein, E., Matsumoto, S., Kelling, S., Merrifield, M., Fink, D., Johnston, A., Hochachka, W.M., Bruns, N.E., Reiter, M.E., Veloz, S., Hickey, C., Elliott, N., Martin, L., Fitzpatrick, J.W., Spraycar, P., Golet, G.H., McColl, C., Low, C., Morrison, S.A., 2017. Dynamic conservation for migratory species. Sci. Adv. 3, e1700707. https://doi.org/10.1126/sciadv.1700707.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484.

Rosen, T., Bath, A., 2009. Transboundary management of large carnivores in Europe: from incident to opportunity. Conserv. Lett. 2, 109–114. https://doi.org/10.1111/j.1755-263X.2009.00054.x.

Runge, C.A., Martin, T.G., Possingham, H.P., Willis, S.G., Fuller, R.A., 2014. Conserving mobile species. Front. Ecol. Environ. 12, 395–402. https://doi.org/10.1890/130237.

Santini, L., Marco, M.D., Visconti, P., Baisero, D., Boitani, L., Rondinini, C., 2013. Ecological correlates of dispersal distance in terrestrial mammals. Hystrix Ital. J. Mammal. https://doi.org/10.4404/hystrix-24.2-8746.

Seidler, R.G., Long, R.A., Berger, J., Bergen, S., Beckmann, J.P., 2015. Identifying impediments to long-distance mammal migrations. Conserv. Biol. 29, 99–109. https://doi.org/10.1111/cobi.12376.

Selva, N., Zwijacz-Kozica, T., Sergiel, A., Olszańska, A., Zięba, F., 2011. Management plan for the brown bear (*Ursus arctos*) in Poland. Warsaw University of Life Sciences, Warsaw, Poland.

Støen, O.-G., Zedrosser, A., Sæbø, S., Swenson, J.E., 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia 148, 356–364. https://doi.org/10.1007/s00442-006-0384-5.

Straka, M., Paule, L., Ionescu, O., Štofík, J., Adamec, M., 2012. Microsatellite diversity and structure of Carpathian brown bears (*Ursus arctos*): consequences of human caused fragmentation. Conserv. Genet. 13, 153–164. https://doi.org/10.1007/s10592-011-0271-4.

Trakhtenbrot, A., Nathan, R., Perry, G., Richardson, D.M., 2005. The importance of long-distance dispersal in biodiversity conservation. Divers. Distrib. 11, 173–181. https://doi.org/10.1111/j.1366-9516.2005.00156.x.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., de Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., de Miranda Mourão, G., Morato, R.G., Morellet, N., Morrison, T.A., Díaz-Muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R.B., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Cunha de Paula, R., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zięba, F., Zwijacz-Kozica, T., Mueller, T., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359, 466–469. https://doi.org/10.1126/science.aam9712.

Zimmermann, F., Breitenmoser-Würsten, C., Breitenmoser, U., 2005. Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. J. Zool. 267, 381–395. https://doi.org/10.1017/S0952836905007545.

Ziółkowska, E., Ostapowicz, K., Radeloff, V.C., Kuemmerle, T., Sergiel, A., Zwijacz-Kozica, T., Zięba, F., Śmietana, W., Selva, N., 2016. Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. Landsc. Ecol. 31, 1863–1882. https://doi.org/10.1007/s10980-016-0368-8.